Development and growth of *Temora longicornis*: numerical simulations using laboratory culture data*

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Abstract

Quantitative expressions are presented to describe the effects of temperature and food concentration on stage duration and growth rate of *Temora longicornis* for each of the model stage groups (N1–N6 – naupliar stages, C1, C2, C3, C4, C5 – the five copepodid stages). The calculations were made on the basis of experimental data from the literature for *T. longicornis* from the south-eastern and the southern North Sea. Relationships were obtained between the growth parameters and temperature for the 5–10°C temperature range and food concentrations from 25 mgC m^{-3} to excess. Also computed was the total mean development time as a function of the above-mentioned parameters, temperature and food availability. The simulations computed here are similar to the experimental results. The growth

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rates for successive stages were obtained according to the correction of the 'Moult Rate' method, which allows the use of mean weights and stage durations. The calculations also suggest that three complete generations of *T. longicornis* from the Gdańsk Deep (the southern Baltic Sea) can develop during a single year.

1. Introduction

Zooplankton is the main component in the diets of herring and sprat, these being the principal fish species caught in the Baltic Sea fishery. The most important components of the sprat's diet are micro- and mesozooplankton – copepods, cladocerans and rotifers. The diet of the herring is dominated by micro- and mesozooplankton in the first period of life, but older fish consume mainly mysidaceans (macrozooplankton) (Załachowski et al. 1975, Wiktor 1990). The copepods in the sprat and herring diet are represented mostly by *Pseudocalanus minutus elongatus*, *Acartia* spp. and *Temora longicornis* (Załachowski et al. 1975, Wiktor 1990). Copepods are the most abundant zooplankton species in the Baltic Sea and adjacent waters.

Numerous environmental factors – most importantly, temperature – govern essential physiological and metabolic processes in copepods. Together with food quality and concentration, this affects mortality rates (Hirst & Kiørbe 2002), egg production (Halsband-Lenk et al. 2002) and the growth and development rates of these animals (Twombly & Burns 1996, Campbell et al. 2001, Peterson 2001, Hirst & Kiørbe 2002, Leandro et al. 2006a,b). In copepods, stage durations decrease and growth rates increase significantly with temperature, causing the animals to develop faster (Leandro et al. 2006a,b). Temperature also has a very important influence on moulting rates in juveniles (Hirst & Bunker 2003).

Experiments on the growth rate of *T. longicornis* suggest that this parameter is directly proportional to food concentration (Harris & Paffenhöfer 1976a,b, Klein Breteler et al. 1982) and is strongly influenced by food quality (Klein Breteler et al. 1990). The development of *T. longicornis* has also been found to accelerate with temperature (McLaren 1978, Martens 1980, Klein Breteler & Gonzalez 1986, Hay et al. 1988, Fransz et al. 1989). However, the combined effect of food concentration and temperature as a function of these parameters on the growth and development rates of *T. longicornis* at each of the model stages (naupliar, C1, C2, C3, C4, C5) is established in this paper. Recently, quantitative expressions describing the effects of temperature and food concentration on the growth and development of *P. minutus elongatus* and *Acartia* spp. were presented by Dzierzbicka-Głowacka (2004, 2005a,b) and Dzierzbicka-Głowacka et al. (2006, 2009a). The experimental data given by Klein Breteler & Gonzalez

(1986) and Klein Breteler et al. (1982, 1990) were sufficient to do likewise for *T. longicornis*.

The present work advances the idea of establishing the combined effect of temperature and food concentration on the development and growth of the naupliar stage and copepodid stages (C1, C2, C3, C4, C5) of *T. longicornis*. It is important to investigate and identify the critical factors in mathematical models of pelagic communities with a high-resolution zooplankton (herbivorous copepods) module as a top-down regulator that may play a significant role in marine ecosystems. In this study the development of copepods *T. longicornis* in the changing environmental conditions in the southern Baltic Sea is modelled. The generation time during the seasons in the upper layer of the Gdańsk Deep (in the southern Baltic Sea) for the 1965–1998 period is determined. Knowledge of the population dynamics of copepods – a major food source for young fish – is essential for prognostic purposes, and a number of such models have been produced recently. This type of study has been carried out for *Pseudocalanus* spp. (Fennel 2001, Dzierzbicka-Głowacka 2005a,b, Stegert et al. 2007, Moll & Stegert 2007) and *Acartia* spp. (Dzierzbicka-Głowacka et al. 2009a,b, 2010b); for *T. longicornis*, however, this will be done in a subsequent investigation.

2. Method

The present analysis is based on data collected from the south-eastern and southern parts of the North Sea (Harris & Paffenhöfer 1976a,b, Klein Breteler et al. 1982, Klein Breteler & Gonzalez 1986, Klein Breteler et al. 1990).

Copepods were collected off the island of Texel (Klein Breteler 1980) with a hand-towed net (diameter 30 cm, mesh size 100 μm) and were subsequently cultivated in the laboratory. All the experiments were carried out in a temperature-controlled environment (15°C) with aged sea water (salinity 28 PSU). Food took the form of *Rhodomonas* sp. and *Isochrysis galbana*. The heterotrophic dinoflagellate *Oxyrrhis marina* was present during the experiments, too. Food concentrations varied from ca 25 to ca 2000 mgC m^{-3} (Klein Breteler et al. 1982).

The calanoid copepod *Temora longicornis* isolated from the Dutch Wadden Sea (Klein Breteler & Gonzalez 1986) was cultured continuously in the laboratory under standard conditions at 15°C and optimal food. Subsequent generations were raised to maturity in four independent experiments, each at a different temperature (5, 10, 15 and 20°C) and a different food level (from 37 to 1420 mgC m^{-3}). Here, too, the source of food was *Rhodomonas* sp. and *I. galbana*.

Adult *T. longicornis* collected off the island of Sylt (Harris & Paffenhöfer 1976a,b) were subsequently maintained in laboratory culture (30 generations). Newly-hatched nauplii were removed from the stock cultures and were reared to adulthood on a diet of the chain-forming diatom *Thalassiosira rotula*. Four mean food concentrations were used: 25, 50, 100 and 200 mgC m^{-3}. The experimental temperature for the copepod cultures and their food was 12.5 ± 0.3°C.

Detailed descriptions of the culture techniques used for *T. longicornis* from the south-eastern North Sea (off Sylt) are given in Harris & Paffenhöfer (1976a,b); similarly, those used for *T. longicornis* from the Dutch Wadden Sea and collected off Texel are described in Klein Breteler (1980), Klein Breteler et al. (1982), and Klein Breteler & Gonzalez (1986).

The weight of a newly-hatched nauplius (N1) used in the present paper is taken after Harris & Paffenhöfer (1976b): it is 0.1 μg ash-free dry weight (AFDW).

Copepod dry weight was converted to carbon using the following conversion factors given by Harris & Paffenhöfer (1976a): 0.3 (nauplii – N1), 0.32 (copepodid – C1), 0.35 (copepodid – C3) and 0.37 (medium adult and adult). These coefficients were the basis for working out the coefficients for the intermediate stages that Klein Breteler (1980) takes account of: 0.3 (N1–N4), 0.31 (N5–N6), 0.32 (C1), 0.355 (C2), 0.35 (C3), 0.36 (C4) and 0.37 (medium adult and adult). The conversion factor of 0.55 after Harris & Paffenhöfer (1976b) was used to convert AFDW to algal carbon.

In the present paper, the relationships between the results from the analysed reports, and temperature and food concentration were found by performing regressions following the appropriate transformation of the data.

2.1. Mean development time

The mean total development time TD (in days) (from N1 to medium adult) was calculated by Klein Breteler & Gonzalez (1986) according to McLaren (1963, 1965) using Bělehrádek's function $TD = a(T - \alpha)^b$. Parameters a and b were obtained by varying α and selecting the regression with the highest correlation coefficient at each food level. These values were given by Klein Breteler & Gonzalez (1986) (see Table III in their paper). Additionally, the development of *T. longicornis* at four temperatures (5, 10, 15 and 20°C) for different food supplies was demonstrated (see Figure 4 in Klein Breteler & Gonzalez (1986)).

McLaren et al. (1969) showed that with $b = -2.05$ the parameter α for 11 species of copepods from the Arctic to the tropics was related to the average environmental temperature and suggested that α might be used in this manner to indicate temperature adaptation.

However, at all food levels, the mean total development time after Klein Breteler & Gonzalez (1986) (see Table III in their paper) was obtained with an average value $b = -0.62$ and $\alpha = 2 - 3$. Assuming this mean value of b for all food levels, the proportionality constant a clearly reflects the effect of food concentration. These parameters differ greatly from those calculated by McLaren (1978) for *T. longicornis* from hatching to 50% adult at excess food (see Table III and Figure 5 in Klein Breteler & Gonzalez (1986)).

Since the three parameters of Bělehrádek's function are dependent on each other, Klein Breteler & Gonzalez (1986) also calculated α and a at food level 1, assuming $b = -2.05$ from McLaren (1963, 1965). Indeed, the resulting $\alpha = -11.7$ and $a = 18091$ show much more resemblance to McLaren's values. The resulting curve fitted only poorly to the measured mean development times, however. At food levels 1/16 and 1/4, the fit was also poor at $b = -2.05$. Therefore, and since at different food levels b did not differ significantly, a stronger curvature seems to be realistic for their copepod population.

McLaren et al. (1969) suggested that thermal acclimation would only affect parameter α. If this is true, the different values of b may point to fundamental physiological differences between different populations of *Temora*. This is in contrast with the observation of those authors that b is constant within closely related species (see p. 82 in Klein Breteler & Gonzalez (1986)).

The stage duration for each model stage (N1–N6 – naupliar stage, C1, C2, C3, C4, C5 – the five copepodid stages) and the generation time using Bělehrádek's function were obtained in the present work in accordance with the data of D (see Figure 4 in Klein Breteler & Gonzalez (1986)). Here, the parameter b was taken from Klein Breteler & Gonzalez (1986); in addition, the values of α calculated in this paper vary from 2 to 3.5 and resemble the values of Klein Breteler & Gonzalez (1986).

Bělehrádek's function was converted to $D = 10^a(T - \alpha)^b$, where the parameters a and b were described as a function of food concentration: $\alpha = a_1 \log Food + b_1$ and $a = a_2 \log Food + b_2$ with the correlation coefficient from 0.69 to 0.97 for the naupliar stage (N1–N6) and the copepodid stage (C1–C5). But the correlation coefficient for a and α as a function of food concentration was too low for all copepodid stages separately (C1, C2, C3, C4, C5). This meant that Bělehrádek's function could not be used to define the mean development times for each copepodid stage separately.

In view of this, the stage duration D in this work was obtained as a function of food concentration and temperature using the minimum development time $D_{\min}$. $D_{\min}$ is the value for which the development rate

is not limited by food availability. The common logarithm of $D_{\min}$ for *T. longicornis* was related linearly to the common logarithm of temperature:

$$\log D_{\min} = a \log T + b. \tag{1}$$

The values of a, b, and r, the correlation coefficients for developmental stages N1–N6, C1, C2, C3, C4 and C5 are given in Table 1. 96% of the

Table 1. Coefficients a and b of equation (1) describing the minimum development time $D_{\min}$ [days] as a function of temperature T [°C] for developmental stages N1–N6, C1, C2, C3, C4, C5, and the N1 – medium adult period ($TD_{\min}$) in *Temora longicornis* (from data given in Klein Breteler & Gonzalez (1986))

Stage	a	b	r
N1–N6	−1.0796	2.2014	−0.9938
C1	−1.0233	1.5073	−0.9836
C2	−1.0154	1.4755	−0.9435
C3	−0.9116	1.3721	−0.9654
C4	−0.6334	1.1521	−0.9212
C5	−0.8972	1.3733	−0.9619
$TD_{\min}$	−0.9827	2.4475	−0.9972

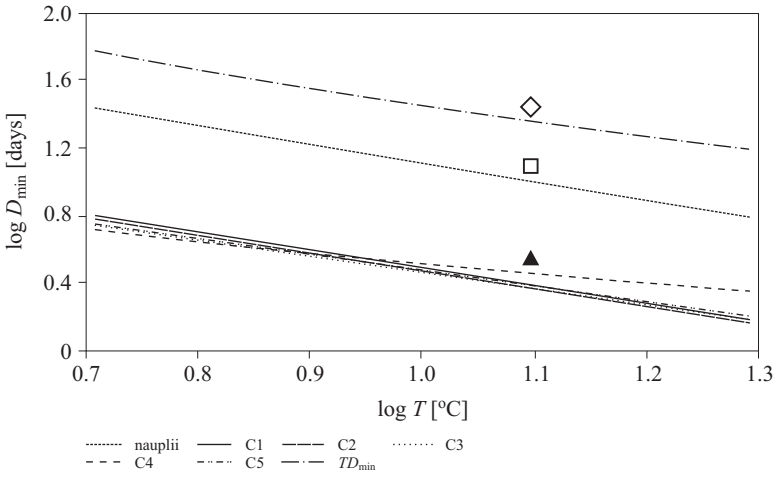

Figure 1. Relationship between minimum development time $D_{\min}$ [days] and temperature T [°C] for different developmental stages (N1–N6, C1, C2, C3, C4, C5) and for the period from N1 to medium adult ($TD_{\min}$) of *Temora longicornis*, obtained after Klein Breteler & Gonzalez (1986), where $TD_{\min}$ is the mean total development time from N1 to medium adult in days; □ – $D_{\min}$ for the naupliar stage, ▲ – $D_{\min}$ for the copepodid stage, ◊ – $TD_{\min}$ – mean total development time (N1–adult) at $T = 12.5$°C and $Food = 200$ mgC m^{-3}, computed here after Harris & Paffenhöfer (1976a,b)

values of $D_{\min}$ computed with equation (1) as a function of temperature lie within the range of the parameter $D_{\min}$ given by Klein Breteler et al. (1982). The regression equations for each of the model stages of *T. longicornis* at temperatures ranging from 5 to 20°C are shown in Figure 1.

The stage duration D of *T. longicornis* for developmental stages N1–N6, C1, C2, C3, C4 and C5, and for the period from N1 to medium adult was also obtained here. It was found to be very sensitive to changes in temperature and food concentration. Conversion of the data for D after Klein Breteler

Table 2. Coefficients a and b of equation (2) describing the mean development time D [days] as a function of food concentration $Food$ [mgC m^{-3}] for developmental stages N1–N6, C1, C2, C3, C4, C5 and the N1 – medium adult period in *Temora longicornis* and at different temperatures T [°C] (from data given in Klein Breteler & Gonzalez (1986))

Stage	Temperature	a	b	r
N1–N6	5	−0.00638	3.7243	−0.9858
	10	−0.01789	3.47189	−0.992
	15	−0.03067	3.58015	−0.9398
	20	−0.00796	2.24512	−0.7917
C1	5	−0.01399	2.6687	−0.9999
	10	−0.1654	2.33563	−0.9979
	15	−0.01151	1.5666	−0.8802
	20	−0.03569	2.30132	−0.956
C2	5	−0.00922	2.06896	−0.979
	10	−0.00989	2.0204	−0.9832
	15	−0.1126	1.86037	−0.988
	20	−0.02051	1.34057	−0.9015
C3	5	−0.00269	1.44253	−0.9056
	10	−0.01032	2.00368	−0.9987
	15	−0.01676	2.19194	−0.9985
	20	−0.01864	1.30412	−0.9293
C4	5	−0.0054	2.27169	−0.9985
	10	−0.01159	1.95198	−0.9809
	15	−0.01454	1.3732	−0.9981
	20	−0.02465	1.62844	−0.9416
C5	5	−0.01386	2.33369	−0.999
	10	−0.00979	2.10051	−0.9768
	15	−0.03485	2.81963	−0.9971
	20	−0.01568	1.13885	−0.8879
TD	5	−0.00857	4.51711	−0.9968
	10	−0.01318	4.24508	−0.9952
	15	−0.02265	4.26934	−0.9889
	20	−0.01383	3.33507	−0.9929

& Gonzalez 1986 – see Figure 4 in this paper) to natural logarithms yielded a linear relationship between time and food concentration. This relationship was described by the equation

$$\ln(D - D_{\min}) = aFood + b; \tag{2}$$

hence,

$$D = e^{aFood+b} + D_{\min}.$$

The values of a, b, and r, the correlation coefficients for developmental stages N1–N6, C1, C2, C3, C4 and C5, and for the total period of growth from N1 to C5 at four temperatures (5, 10, 15 and 20°C) are listed in Table 2.

The coefficients a and b of the equations describing D as a function of food concentration were obtained as a function of temperature in the 5–20°C range by a third-degree polynomial, because the correlation coefficient was too low to use linear-log or linear-exp regression on the data for a and b. The regression equations for each of the stages N1–N6, C1, C2, C3, C4, C5 and for the total period of growth from N1 to medium adult are given in Table 3. By substituting a and b in equation (2) for the equations in Table 3,

Table 3. Coefficients a and b of equation (2) describing the mean development time D [days] as a function of temperature T [°C] in developmental stages N1–N6, C1, C2, C3, C4, C5 and the N1 – medium adult period (TD) in *Temora longicornis*, computed here from data given in Klein Breteler & Gonzalez (1986); correlation coefficients $r^2 \approx 1$

Developmental stage	Coefficients a and b
N1–N6	$a = 0.00005T^3 - 0.0015T^2 + 0.0116T - 0.0329$ $b = -0.0024T^3 + 0.0794T^2 - 0.8201T + 6.1413$
C1	$a = -0.00005T^3 + 0.0016T^2 - 0.0163T + 0.0329$ $b = 0.0026T^3 - 0.0863T^2 + 0.7754T + 0.6262$
C2	$a = -0.00001T^3 + 0.0003T^2 - 0.0026T - 0.0021$ $b = -0.0011T^3 + 0.0438T^2 - 0.5878T + 4.6557$
C3	$a = 0.000004T^3 - 0.0001T^2 - 0.0006T + 0.0028$ $b = -0.0009T^3 + 0.0207T^2 - 0.0337T + 1.2117$
C4	$a = -0.00001T^3 + 0.0005T^2 - 0.006T + 0.0144$ $b = 0.0015T^3 - 0.0489T^2 + 0.4146T + 1.2392$
C5	$a = 0.0001T^3 - 0.0035T^2 + 0.0365T - 0.1204$ $b = -0.0045T^3 - 0.1531T^2 - 1.5615T + 6.8714$
TD	$a = 0.00003T^3 - 0.001T^2 + 0.009T - 0.032$ $b = -0.0017T^3 + 0.0561T^2 - 0.6034T + 6.3402$

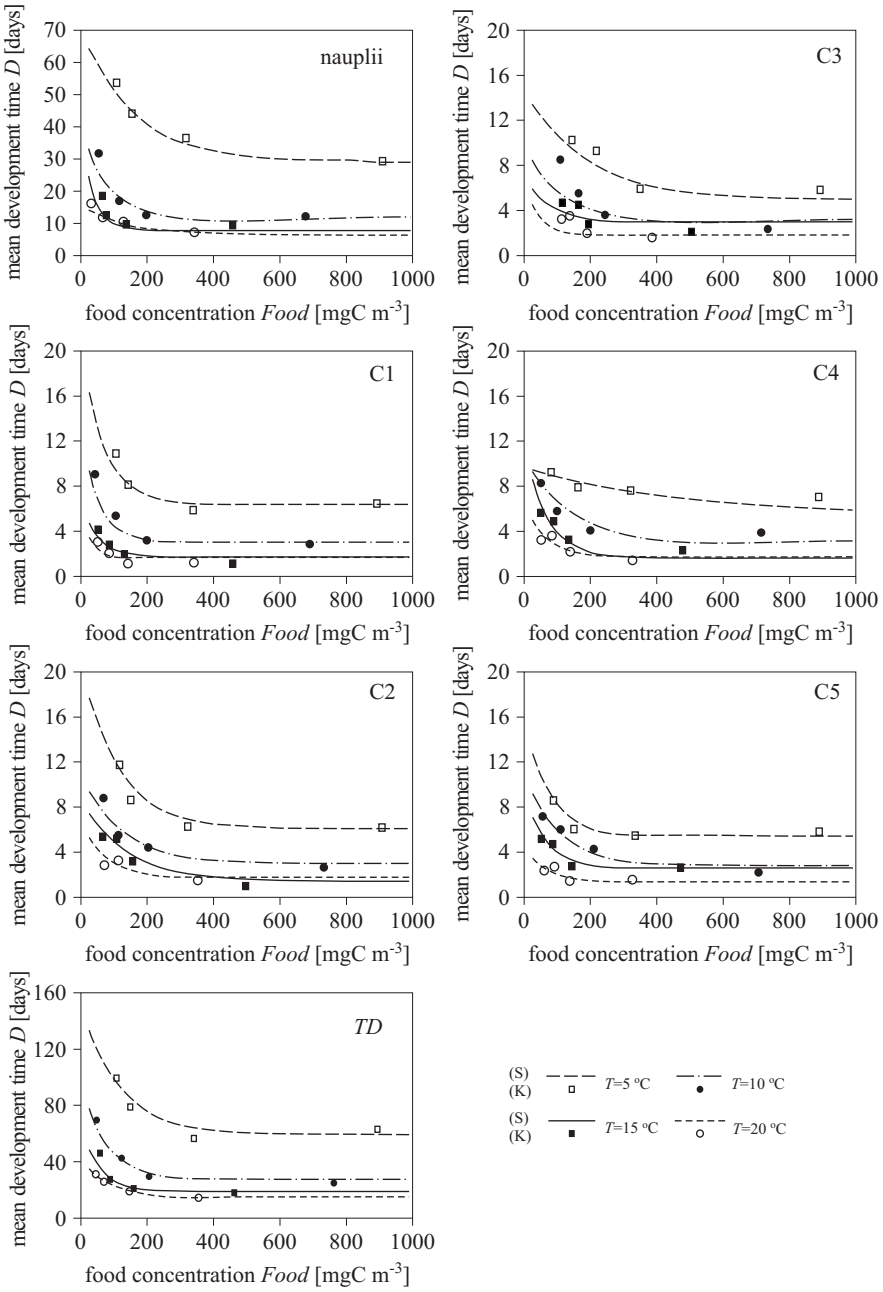

Figure 2. Relationships between mean development time D [days] for each of the model stages of *Temora longicornis* and temperature T [°C] at different temperatures (5, 10, 15 and 20°C) for naupliar stages N1–N6, copepodid stages C1, C2, C3, C4 and C5, and mean total development time TD (in days); (S) – simulated results, (K) – data after Klein Breteler & Gonzalez (1986)

D in the studied stages of *T. longicornis* becomes a function of both food concentration from 25 mgC m^{-3} to excess and temperature in the 5–20°C range. 93% of the values of D computed with equation (2) as a function of food concentration and temperature lie within the range of the parameter D given by Klein Breteler et al. (1982). The sets of stage duration curves computed with equation (2) of *T. longicornis* for each of model stages are shown in Figure 2.

On the basis of data from Harris & Paffenhöfer (1976a,b), the stage duration D for different food concentrations *Food* (25, 50, 100, 200 mgC m^{-3}) at a temperature of 12.5°C was also obtained. The calculations were made using a formula rewritten as $D = 1/k \ln(W_{i,\,\mathrm{entry}}/W_{i,\,\mathrm{exit}})$, where k is the coefficient of daily exponential growth for different developmental periods (see Table 5 in Harris & Paffenhöfer (1976a)), and $W_{i,\,\mathrm{entry}}$ and $W_{i,\,\mathrm{exit}}$ are the mean weights of animals entering and leaving stage i, which were obtained on the basis of the weight increment (see Table 1 in Harris & Paffenhöfer (1976b)).

The stage duration D described by equation (2) according to the data given by these authors was not available, because the differences between the values of D and D_{min} in the 25–200 mgC m^{-3} range of food concentration were too low. Thus, transformation of these data to a base 10 logarithm

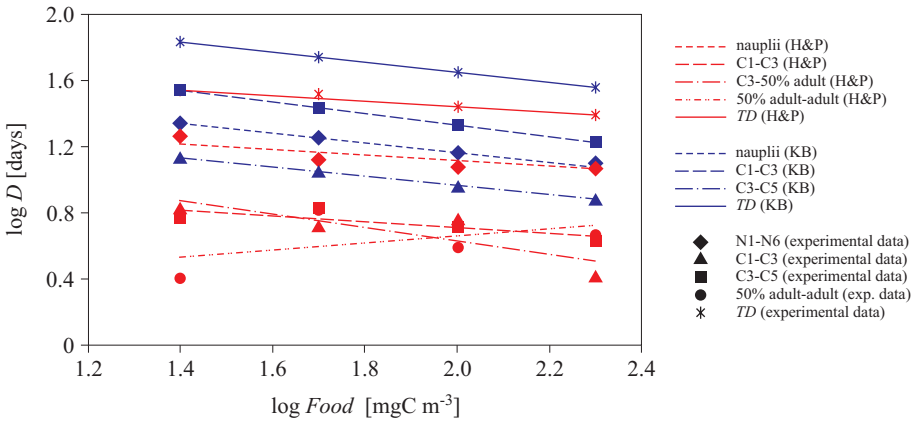

Figure 3. Relationship between mean development time D [days] and food concentration *Food* [mgC m^{-3}] in the 25–200 mgC m^{-3} range at a temperature of 12.5°C for different developmental stages: N1–N6, C1, C2, C3, C4, C5, and N1 – medium adult (TD) of *Temora longicornis* obtained on the basis of data from Harris & Paffenhöfer (1976a,b) (H) (red lines) and Klein Breteler & Gonzalez (1986) (K) (blue lines); ♦ – N1–N6, ■ – C1–C3, ▲ – C3–C5, • – 50% adult–adult ∗ – TD; red – after Harris & Paffenhöfer (1976a,b); blue – after Klein Breteler & Gonzalez (1986)

gives a linear relationship between food concentration and the value of D at a temperature of 12.5°C: $\log D = a \log Food + b$. The regression equations (red lines) together with the results of D obtained here after data taken from Klein Breteler & Gonzalez (1986) at 12.5°C (blue lines) are shown in Figure 3.

2.2. Growth rate

Weight-specific daily growth rates of length class i (field samples) or stage i (experiments) were derived by Klein Breteler et al. (1982) according to $1/D_i \ln(W_{i+1}/W_i)$, where D_i is the development rate per individual, and W_i is the AFDW as estimated from the length-weight relation of the cultured copepods (see Table I in Klein Breteler et al. (1982)). However, according to Hirst et al. (2005), the growth rate should be determined from the point of entry $W_{i,\,\mathrm{entry}}$ to the exit stage $W_{i,\,\mathrm{exit}}$ by the equation $1/D_i \ln(W_{i,\,\mathrm{exit}} W_{i,\,\mathrm{entry}})$, which thus includes the moult rate. These entry and exit data are not given in Klein Breteler's data set. Therefore, the other approach given by Hirst et al. (2005), which allows the use of such mean stage weight data, is included in our calculations. This correction of the 'Moult Rate' method (see equation (22) in their paper) is described by

$$\ln(W_{i+1}/W_i) \Big/ (D_i + D_{i+1})/2 = g_{i\to i+1} + \tag{3}$$
$$+ \Big[\ln h_o(g_{i\to i+1}, D_{i+1}) - \ln h_o(g_{i\to i+1}, D_i) \Big] \Big/ (D_i + D_{i+1})/2,$$

where the function $h_o(g, D)$ is given by $h_o(g, D) = [\exp(gD/2) - \exp(-gD/2)] /(gD)$. Hence, this equation describes growth using arithmetic mean weights and stage durations of consecutive (moulting) stages (Hirst et al. 2005).

According to the data for D_i at 15°C and excess food, the maximum growth rates of *T. longicornis* for nauplii, C1–C3 and C3–C5 were obtained by the numerical solution of equation (3), where W_i is the mean body weight for successive stages, D_i is the stage duration and $g_{i\to i+1}$ is an unknown quantity. Equation (3) was solved by following the procedure below to give $g_{i\to i+1}$:

step 1: read W_i, W_{i+1}, D_i, D_{i+1};

step 2: $g_{i\to i+1} = 0.0001$;

step 3: if LH = RH then $g_{i\to i+1} := g_{i\to i+1}$ else $g_{i\to i+1} := g_{i\to i+1} + 0.0001$ go to step 3 where LH and RH are the left- and right-hand sides of equation (3) respectively.

In this paper, the mean growth rate of *T. longicornis* for three developmental stages (N1–C1, C1–C3 and C3–C5) as a function of food concentration at 15°C is given by the equation:

$$g_i = g_{\max} fte \left\{ 1 - \exp\left(\frac{-(Food - Food_o)}{k_{Food}} \right) \right\}, \tag{4}$$

where $g_{\max}$ (% of weight day^{-1}) is the maximum growth rate at 15°C and excess food (see equation (3)), $Food$ (mgC m^{-3}) is the food concentration, $Food_o$ (mgC m^{-3}) is the value of $Food$ at which $g = 0$, and k_{Food} (mgC m^{-3}) is the half-saturation constant, since $g_{\max}/k_{Food}$ for $Food$ is slightly greater than $Food_o$, and fte is a function of temperature. For each stage, $Food_o = 0$ and $fte = 1$ at $T = 15$°C; however, k_{Food} lies in the 90–140 mgC m^{-3} range and is described by:

$$k_{Food} = (-0.0001(\log Food)^3 + 0.0016(\log Food)^2 - 0.0068 \log Food + \\ + 0.0162)^{-1}$$

for the naupliar stage ($r^2 = 0.9607$), and

$$k_{Food} = (-0.0001(\log Food)^3 + 0.0019(\log Food)^2 - 0.0082 \log Food + \\ + 0.0173)^{-1}$$

for the copepodid stages ($r^2 = 0.9519$).

Growth rate values in the developmental classes at 15°C for different food supplies found by Klein Breteler et al. (1982) and computed here with equation (4) are shown in Figure 4. The dependence of the growth rate on temperature can be described by the equation:

$$fte = ft_1 ft_2, \tag{5}$$

where

$$ft_1 = t_1 t_2^T,$$

$$ft_2 = \begin{cases} 1 & T \le T_o \\ 1 - \left(\frac{T - T_o}{t_3 T_o} \right)^{P1} & T \ge T_o \end{cases}$$

and $fte = 1$ for $T = T_o$. The function fte for temperatures over T_o is modified by part of ft_2.

In this paper, the influence of temperature on growth rate is described by equation (5) representing a Q_{10} value of 2.274 applicable to the temperature range of 5–15°C. The temperature coefficient Q_{10} was calculated according to the data given by Klein Breteler & Gonzalez (1986). The t_2 coefficient

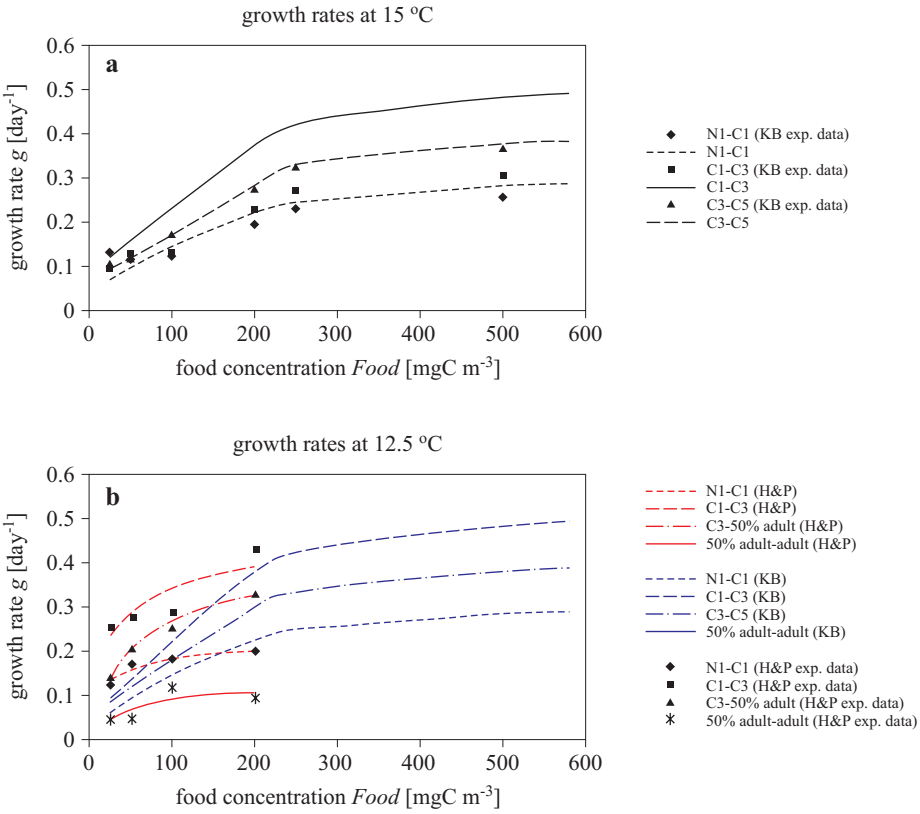

Figure 4. Relationship between the growth rate g [day^{-1}] and food concentration *Food* [mgC m^{-3}] for three developmental stages of *Temora longicornis* (naupliar stage, early copepodid stages (C1–C3) and larger copepodid stages (C3–C5)) computed by equation (4) (lines) and data from Klein Breteler et al. (1982) and Harris & Paffenhöfer (1976b) at 15°C (a) at 12.5°C (b)

was equal to 1.0856 based on Q_{10}. Coefficient t_1 was calculated so that fte was equal to 1 at 15°C; t_1 was therefore equal to 0.292. Coefficients t_1 and t_2 were identical for all stages.

Additionally, the parabolic threshold function ft_2 (with $T_o = 15$°C, $t_3 = 0.6$ and $P1 = 1.3$) describes a decrease at higher temperatures as a result of physiological depression. Growth therefore follows an exponential curve up to the optimal temperature of ca 15°C and decreases at higher temperatures.

Using the function fte, the growth rate of *T. longicornis* for three developmental classes (N1–C1, C1–C3 and C3–C5) as a function of food concentration for different temperatures was obtained with the aid of equation (4) and is shown in Figure 5. The growth rate at 12.5°C was also

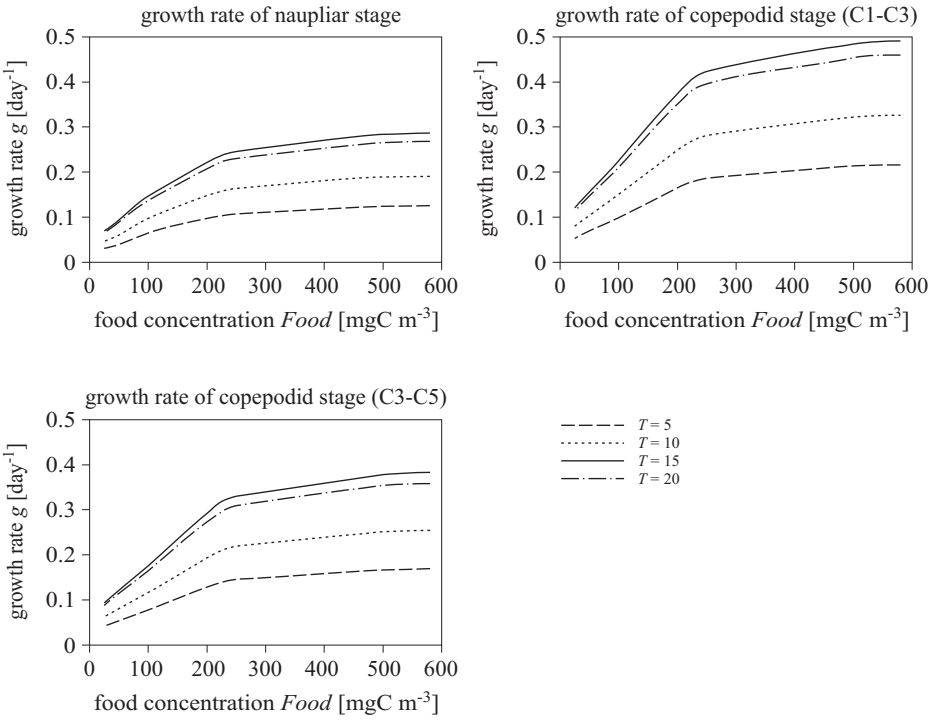

Figure 5. Relationship between growth rate g [day^{-1}] and food concentration $Food$ [mgC m^{-3}] at four temperatures for different developmental stages of *Temora longicornis* (naupliar stage, early copepodid stages (C1–C3) and larger copepodid stages (C3–C5)), computed here using equation (4)

computed and compared with the results obtained by Harris & Paffenhöfer (1976a, see Table 5 in that paper) (see Figure 6) – see Discussion.

3. Results

3.1. Mean development time

The computed results show that the minimum stage duration, $D_{\min}$, for *Temora longicornis*^{KB} (KB stands for *Temora longicornis* after Klein Breteler & Gonzalez (1986)) increased with falling temperature. For the copepodid stages, $D_{\min}$ values for *T. longicornis*^{KB} were similar at different temperatures and fell slightly with advancing stage of development. But for stage C4, $D_{\min}$ was higher only at high temperatures (see Figure 1).

The stage duration for *T. longicornis*^{H} (H stands for *Temora longicornis* after Harris & Paffenhöfer (1976a,b)) for $Food = 200$ mgC m^{-3} at 12.5°C fell slightly with increasing copepodid stages, as in the case of *T. longicornis*^{KB}. The mean value of $D_{\min}$ for the copepodid stages is given in Figure 1.

The minimum total stage duration $TD_{\min}$ for the stages from N1 to C5 of *T. longicornis*^{KB} (23.42 days) and from N1 to 50% adult of *T. longicornis*^{H} (24.65 days) was similar for these species at 12.5°C. A slight difference in $D_{\min}$ (ca 2.4 days) was also found between these two species for the naupliar stage; $D_{\min}$ was 10.4 days and 12.82 days for *T. longicornis*^{KB} and for *T. longicornis*^{H} respectively. But for the copepodid stages, $D_{\min}$ values were a little higher (see Figure 1).

Figure 2 provides comprehensive information on the effects of interactions between temperature and developmental stage on stage duration in *T. longicornis*^{KB}. The results indicate that the effect of increasing food shortened the average time to reach each stage D to the minimum value $D_{\min}$ at all temperatures. The decrease in D was explicit at low food concentrations (< 100 mgC m^{-3}) in all the model stages. Mean development time tends to a constant value $D_{\min}$, as food concentrations approach high values ($Food > 350$ mgC m^{-3} for nauplii and the younger copepodids C1, C2 and C3; $Food > 300$ mgC m^{-3} for the older copepodids C4 and C5). Generally, the duration of all stages decreased with increasing temperature in the studied range of food concentration. But at higher food concentrations ($Food > 100$ mgC m^{-3} for nauplii and > 200 mgC m^{-3} for copepodids C1, C2 and C4), D was inversely related to temperature only in the 5–15°C range.

For other copepodid stages (C3 and C5), the critical temperature of 15°C did not occur and the stage duration decreased with temperature rising to 20°C. But in these developmental stages, there were slight differences in D at 10°C and 15°C according to the data in Klein Breteler & Gonzalez (1986). We suggest that the values of D for C3 and C5 at 15°C are too low.

The influence of food concentration at different temperatures on TD was similar to D for each stage duration, as described above. TD was inversely related to temperature in the range from 5 to 20°C. But the values of TD were nearly equal at both 15°C and 20°C. The calculations show that for the growth period from N1 to C5, when food is in excess, *T. longicornis* lives longer at lower than at higher temperatures. The total stage duration N1–C5 is ca 130 days at 5°C and ca 50 days at 15°C when the population is starving ($Food = 25$ mgC m^{-3}); however, it is ca 70 days at 5°C and 18 days at 20°C as the food concentration rises to high values, at which the growth rate tends to become constant ($Food = 350$ mgC m^{-3}). Hence, at low temperature and food concentration ($T = 5$°C, $Food = 25$ mgC m^{-3}), the individual reaches maturity only after some considerable time (ca 140 days), assuming that D of adults is about 10 days, not including the former time span. At high temperatures and high food concentrations ($T = 20$°C,

$Food = 350$ mgC m^{-3}), however, animals reach maturity after just 20 days (assuming that D of adults is about 2 days).

Figure 3 shows clearly the effect of food concentration on the stage duration of *T. longicornis*^{H} for all the developmental classes – nauplii (N1–C1), younger copepodids (C1–C3), older copepodids (C3–50% adult) and adults (50% adult to adult) – and on the mean total development time (N1–adult) according to the data in Harris & Paffenhöfer (1976a,b) (black lines). Stage duration became shorter with increasing developmental stage and the average time to reach each stage D decreased with increasing food concentration, except the 50% adult developmental stage, in which D increased with rising $Food$. However, for the copepodid stages (C1–C3 and C3–50% adult), D were similar.

3.2. Growth rate

The results indicate that the growth rates for the three developmental stages (N1–C1, C1–C3, C3–C5) of *T. longicornis*^{KB} obtained in this work as a function of food concentration at 15°C are similar to those given by Klein Breteler & Gonzalez (1986) (see Figure 4a), except for one stage – the early copepodids (C1–C3) – for which g is 50% higher (ca 0.2 day^{-1}) at excess food; however, for nauplii, g is insignificantly higher (ca 0.03 day^{-1}) and for older copepodids (C3–C5) it is equal to the results obtained here. The difference in growth rate for stage C1–C3 is caused by the fact that Klein Breteler & Gonzalez (1986) used the mean weights W_i and W_{i+1} of stages i and $i+1$ respectively to calculate g after $1/D_i \ln(W_{i+1}/W_i)$. The problems with growth rate estimates in juvenile copepods are described in detail by Hirst et al. (2005).

Figure 5 clearly shows the effects of interactions between temperature and food concentration on the growth rate of *T. longicornis*^{KB} for each model stage (N1–C1, C1–C3, C3–C5) according to the data of D at 15°C after Klein Breteler & Gonzalez (1986) and the function fte. The increase in g with every next developmental stage is not observed, and g assumes the highest values for the younger copepodids (C1–C3). The increase in g with temperature in the 5–15°C range is explicit. But for temperatures above 15°C, there is a slight decrease in g according to the parabolic threshold function ft_2. In the present work, the calculated $g_{\max}$ of *T. longicornis*^{KB} for three stages (naupliar, early and older copepodid) were 0.128, 0.22 and 0.172 day^{-1} at 5°C, 0.192, 0.332 and 0.259 day^{-1} at 10°C, 0.291, 0.512 and 0.392 day^{-1} at 15°C, and 0.271, 0.468 and 0.365 day^{-1} at 20°C respectively.

The growth rate rose with increasing food concentration for all periods of development. For example, in the larger copepodid stages (C3–C5) at 12.5°C, the computed g of *T. longicornis*^{KB} was 0.094 day^{-1} at

$Food = 25$ mgC m^{-3}, 0.122 day^{-1} at $Food = 50$ mgC m^{-3}, 0.169 day^{-1} at $Food = 100$ mgC m^{-3}, 0.293 day^{-1} at $Food = 200$ mgC m^{-3} and 0.378 day^{-1} at $Food = 500$ mgC m^{-3}. However, for $Food < 250$ mgC m^{-3}, the influence of temperature on growth rate at all stages declined with decreasing food concentration. The changes in the growth rate with variations in temperature and food concentration were more pronounced at high temperatures (> 10°C) and lower food levels (< 250 mgC m^{-3}). The curves ran almost parallel, and the differences between the curves at low food levels (< 50 mgC m^{-3}) were only slight.

The growth rates of *T. longicornis*^{H} for three developmental stages and the regression equations for these data were obtained using the results given by Harris & Paffenhöfer (1976a) at 12.5°C in the 25–200 mgC m^{-3} range of food concentration (see Figure 4b).

The increase in g with rising food concentration was explicit but was not observed with increasing developmental stage. The value of $g_{\max}$ (for $Food = 200$ mgC m^{-3}) of *T. longicornis*^{H} for the younger copepodids was the highest (0.43 day^{-1}) and it was around twice as high as that for nauplii, ca 1.3 times as high as that for the older copepodids and ca four times as high as that for adults. However, the value of $g_{\max}$ (for $Food = 200$ mgC m^{-3}) of *T. longicornis*^{KB} for the younger copepodids was also the highest (0.374 day^{-1}) and it was ca 1.71 as high as that for nauplii, ca 1.33 times as high as that for the older copepodids. The differences in g of *T. longicornis*^{H} between the stages increased with declining food level, unlike *T. longicornis*^{KB} for which this drop was considerable.

4. Discussion

Several interactions of broad biological and ecological significance were found in the present study. The authors have made an attempt to formulate some general statements about growth processes in *Temora longicornis* by integrating the experimental data of Klein Breteler et al. (1982) and Klein Breteler & Gonzalez (1986) with those in papers of Harris & Paffenhöfer (1976a,b).

The values of D computed here for *T. longicornis*^{KB} at each of the model stages are similar to the original results obtained by Klein Breteler et al. (1980, 1982) and Klein Breteler & Gonzalez (1986) at the same range of temperature and food concentration. The slight differences in TD were less at higher temperatures than at lower ones under similar food conditions and were due to the difference in food concentration.

On the basis of these results it should be noticed that the development of *T. longicornis* is not isochronal, even at optimal food concentrations (Klein Breteler & Gonzalez 1986). Deviations from the isochronal pattern

of development have been noted in other species of calanoid copepods too – *Acartia* spp., *Centropages* spp. and *Eurytemora* spp. (Peterson 2001, Leandro et al. 2006a,b). The first naupliar stage has a short duration. Development is prolonged at the N2 stage and at the C4 and C5 stages. Stage durations are approximately equal through the late naupliar stages and early copepodid stages.

The present study has also demonstrated that the mean development time for each of the model stages of *T. longicornis*^{KB} is a function of both temperature in the 5–20°C range and food concentration from 25 mgC m^{-3} to excess, rising with decreasing temperature and food level in the studied ranges, except for some developmental stages (naupliar stages, C1, C2 and C4) for which the temperature of ca 15°C was the optimum value.

Differences in D at 12.5°C were found between *T. longicornis*^{KB} and *T. longicornis*^{H} in similar stage groups. The slight difference in D between the two species at the naupliar stage was from 1 (under conditions of excess food) to 4.7 days and depended on the food concentration. But D of *T. longicornis*^{KB} was four times and twice as long as that of *T. longicornis*^{H} for early (C1–C3) and larger (C4–C5) copepodid stages respectively in the 25–200 mgC m^{-3} range of food concentration. TD of *T. longicornis*^{KB} was twice as long as TD of *T. longicornis*^{H}. For example, at $Food =$ 25 mgC m^{-3}, TD was 68.62 days for *T. longicornis*^{KB} and 33.705 days for *T. longicornis*^{H}.

In the present study, the generation time N1–C5 for *T. longicornis*^{KB} at all temperatures was shorter than the values found by other authors, i.e. the difference in TD is ca 12% (4 days) and 25% (9 days) at ca 10°C according to the data given by Hay et al. (1988) and McLaren (1978) respectively. However, at 20°C, it was 26.2% (5.5 days) when results from the German Bight after Martens (1980) and the experimental data given by Person-Le Ruyet (1975) were included. Fransz et al. (1989) stated that the respective average times required for the development of *T. longicornis* from the Southern Bight of the North Sea was 45, 35 and 50 days in the 5–10°C, 7–12°C and 12–18°C temperature ranges. The values were obtained on the basis of field samples at different temperatures for three generations. The differences in TD between the generations were caused by different food sources, food concentrations and temperatures.

To compare the influence of food and temperature on the growth rate of *T. longicornis*^{KB} five calculation runs were done for 5, 10, 12.5, 15 and 20°C at different food levels. The impact of temperature on growth rates was defined by the function fte, which at lower temperatures (< 15°C) is described by Q_{10} and at higher ones by the parabolic threshold function ft_2. The growth rate of *T. longicornis*^{KB} increases rapidly with rising

temperature in the 5–15°C range but less so with a food concentration from 25 mgC m^{-3} to excess. But the growth rates for the model stages were nearly equal at both 15°C and of 20°C according to the function fte. Figure 5 shows that the optimum temperature for the development of *T. longicornis* is slightly higher than 15°C. In the real environment during summer, in the 15–20°C temperature range, and probably with limited food availability, an increase in temperature reduces growth of almost all developmental stages.

The growth rate of *T. longicornis*^{H} at 12.5°C in the 25–200 mgC m^{-3} range of food concentration was also obtained here after data given by Harris & Paffenhöfer (1976a,b). If we compare our results of g for *T. longicornis*^{KB} at 12.5°C to the same stage groups as in their studies and assume that N1 does not grow, it appears that those authors probably found values similar to (*Temora*) or higher than (*Pseudocalanus*) those found by Klein Breteler et al. (1982) at the same food concentration and temperature (see pp. 205–206 in Klein Breteler et al. 1982).

The values of g for *T. longicornis*^{H} except the naupliar stages are higher than those for *T. longicornis*^{KB} at 12.5°C, which were computed using the equation given by Hirst et al. (2005) and according to the Q_{10} coefficient. On the basis of the findings and analysis in this study, differences in g are found between the two species and are smaller if the correction by Hirst et al. (2005) is included. The growth rate of *T. longicornis*^{H} is from 1.15 to 2.4 times higher than g for *T. longicornis*^{KB} and depends on development stage and food concentration; for example, for early copepodids assuming $Food = 200$ mgC m^{-3}, g is equal to 0.43 day^{-1} and 0.374 day^{-1}, and for $Food = 25$ mgC m^{-3}, g is equal to 0.24 day^{-1} and 0.121 day^{-1} respectively. It is more probable that the difference between the results found by these authors is explained by the different algae used as food and other conditions of the experiments.

The quality and quantity of food available to copepods is very important for their growth and development. In natural conditions copepod diets are selective and diverse. Selectivity by copepods may relate to the size of the prey (Atkinson 1995), its toxicity (Huntley et al. 1986) and nutritional quality (Houde & Roman 1987). Copepods often consume not just phytoplankton but heterotrophic flagellates and ciliates, detritus and other metazoans, and they can feed cannibalistically (Hirst & Bunker 2003).

In the studies that our parameterization is based on (Klein Breteler et al. 1982, Klein Breteler & Gonzalez 1986, Klein Breteler et al. 1990), three different sources of food were used: *Isochrysis galbana*, *Rhodomonas* sp. and a mixture of these algae with *Oxyrrhis marina*. In the laboratory studies of *Pseudocalanus elongatus* and *T. longicornis*, Klein Breteler et al. (1990)

suggested that the development was not dependent on the type of food used in experiments. Only with *I. galbana* was the development of *T. longicornis* clearly retarded (especially during the copepodid stages) (see Figure 2 in Klein Breteler et al. 1990).

However, the quality of food is also closely related to the copepod's stage of development (Gruzov 1985, Klein Breteler et al. 1990). The flagellate *O. marina* has a low food value for nauplii, owing to its large size, but is the main food for the copepodid stages. For optimal growth, the naupliar and early copepodid stages depend largely on alternative smaller food like *Rhodomonas* sp. and *I. galbana*. Additionally, the growth of the naupliar stages may be slower because of their poorer ability to handle and ingest small food particles (Fernández 1979), since the only functioning mouthparts are the first and second antennules and mandibles. In the N6, these buds become greatly enlarged, and with the moult to C1, all of the mouthparts unfold (Peterson 2001).

According to recent evidence, the growth and development rates of copepods may also depend on the area of occurrence. Different populations may develop slightly different survival strategies to adapt to their habitat. Two different populations exhibit different development rates when reared at the same temperature. There are differences in growth rates between populations too, particularly when reared at high temperatures with the population acclimated to cold temperatures growing faster than the warm acclimated population. Additionally, populations show different ontogenetic responses to temperature shifts (Leandro et al. 2006a).

In this paper, the development of individuals in the southern Baltic Sea is manifested by a change in the total stage duration (N1–C5) as a function of both temperature and food concentration.

The impact of the above parameters on the generation time of *T. longicornis* during the seasons in the upper 10 m layer in the Gdańsk Deep (southern Baltic Sea) is described by equation (2). This approach is possible because *T. longicornis* is not very sensitive to differences in salinity – like some *Acartia* species, it is a euryhaline species – but unlike *P. elongatus*, which is a stenohaline species. The temperature and food composition (equal to 60% of the phytoplankton biomass, 15% of the zooplankton biomass and 25% of the pelagic detritus concentration) used in this paper are mean values from the last 38 years (1965–98) (data from the 1DCEM model – Dzierzbicka-Głowacka et al. 2006, 2010a). For the population of *T. longicornis*, food – a mixture of phytoplankton, zooplankton and detritus – results in an available food concentration that increases considerably to 180 mgC m^{-3} at the beginning of April, but drops to 100 mgC m^{-3} by the end of June. The comparatively high food level is maintained

during the summer. When the temperature reaches its maximum, the food concentration assumes a value of about 150 mgC m^{-3} by the end of August (see Figure 6a).

The annual cycle of the generation time as a result of the above-mentioned parameters is shown in Figure 6b. The simulated mean total development time of *T. longicornis* during the seasons in the southern Baltic Sea is in the 120–48 day range during the spring bloom, i.e. at 4–10°C with an excess of food, ca 40 days in summer and from 140 to 250 days in winter conditions. The influence of temperature and food availability on the duration of developmental stages in *T. longicornis* is much the same as in the case of *Acartia* spp. from the southern Baltic Sea (Dzierzbicka-Głowacka et al. 2009a), except during the spring bloom, when the simulated generation time of *T. longicornis* is shorter than TD of *Acartia* spp., ca 12 days on average. The best conditions for the development of *T. longicornis* are in the spring/summer and summer/autumn, but for *Acartia* spp. definitely in the summer.

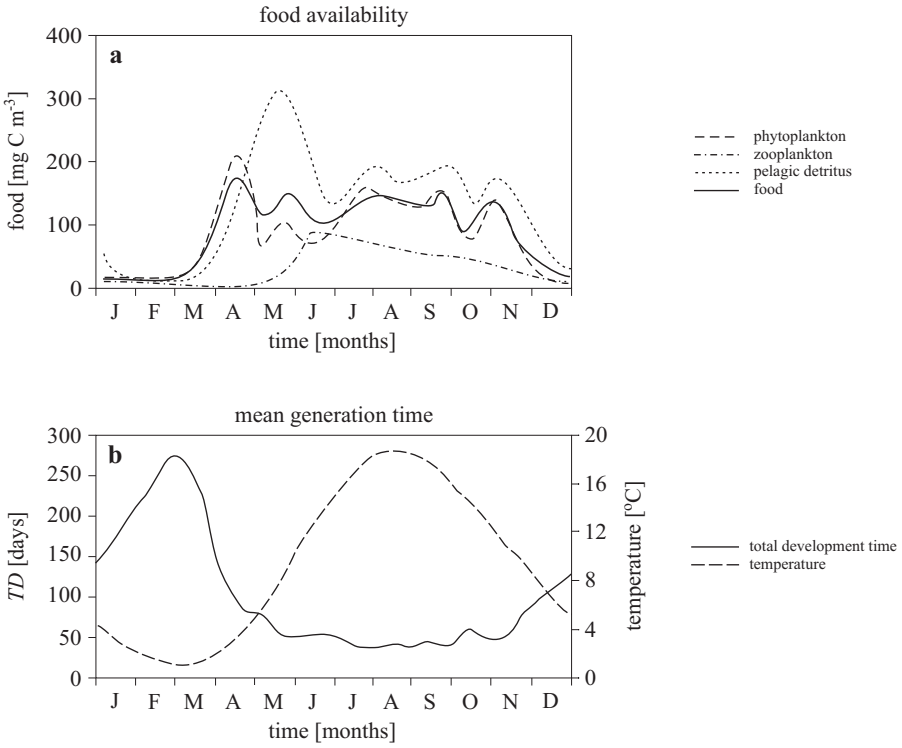

Figure 6. Simulated forcing and development of zooplankton for the annual cycle in the Gdańsk Deep; mean food availability (a), mean generation time of *Temora longicornis* (b)

The calculations also suggest that three complete generations of *T. longicornis* from the Gdańsk Deep can develop during a single year in the upper layer. Simulated generation times are affected mostly by temperature and to a lesser degree by food availability. But in the spring bloom time, the effect of food concentration on the first generation is more evident.

The complete mean development time of *T. longicornis* in the southern Baltic Sea at temperatures below 10°C is longer, and in the 7–12°C temperature range is unchanged, but at higher temperatures it is shorter than the value found by Fransz et al. (1989) for three generations. The respective differences in TD between these results are ca 5 days, 0.5 day and 10 days. They are probably caused by the food concentration, which depends on the composition used in the numerical calculations.

T. longicornis is a eurythermic copepod species that has a wide geographic range – from temperate to arctic waters. In the North Sea and adjacent waters, i.e. the Baltic Sea and the English Channel, the copepod *T. longicornis* is one of the more abundant zooplankton species. Knowledge of their life parameters (e.g. development time, growth rate and egg production) provides fundamental information on energy and matter transformation in pelagic food webs. These organisms play a dominant role in marine food webs and biogeochemical cycles of organic matter.

The model parameters obtained here from a synthesis of corrected laboratory culture data and simulations can be used to investigate the effects of climate change on the life cycle development of *T. longicornis* and factors that have consequences for its role in the food web dynamics. This is the first main step in studies of copepods in understanding how the population dynamics of a dominant species interacts with the environment.

Our means of simulation could be used for other species, both marine and freshwater, e.g. the data for the copepod *Boeckella triarticulata* (Twombly & Burns 1996) like those from Klein Breteler (see section 2) could be used to test the model.

The next step in our studies will be to determine the egg production by female of *T. longicornis* based on the hypothesis that the food-saturated rate of production of egg matter is equivalent to the specific growth rate. The copepod model will be calibrated for *T. longicornis* under the environmental conditions typical of the southern Baltic Sea, including the influence of salinity as a masking factor on its development. Another step in our work is to run the population model within an ecosystem model (Dzierzbicka-Głowacka et al. 2010a) to study the impact of seasonal variations of food and temperature as well as salinity on the *T. longicornis* biomass in the southern Baltic Sea.

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